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Soil properties and microbial processes in response to land-use change in agricultural highlands of the Central Andes

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Abstract

Understanding changes in soil functions in response to land-use change is important for guiding agricultural practices towards sustainable soil management. We evaluated the differences in soil properties (soil organic matter, water extractable carbon (C) and nitrogen (N), microbial biomass, pH_{KCL} and exchangeable cations) and microbial processes (respiration potential, net N mineralization, net nitrification and metabolic potential of soil bacteria), as well as the relative importance of soil properties in explaining changes in processes under three land uses (potato crops, fallow fields and eucalyptus plantations) in the agricultural highlands of the Central Andes. Soils under potato crops were characterized by the highest net N mineralization and net nitrification rates, and extractable phophorus (P), and the lowest microbial biomass P. Conversion to eucalyptus plantations led to an increase in soil organic matter, water extractable C and microbial biomass, and a decrease in extractable P and metabolic diversity of soil bacteria. Higher exchangeable aluminium (Al) indicated soil acidification under eucalyptus. Fallow practices did not lead to major changes in soil properties and microbial processes, indicating that fallow practices for up to 6 years were too short to substantially contribute to soil fertility restoration. Hot water extractable carbon (HWC) showed the best relationship with soil processes (respiration potential, net N mineralization and net nitrification). Our results highlight the necessity of alternative management practices for maintaining soil fertility under potato crops, the drastic modification of soil properties and processes under eucalyptus plantations, and the potential of HWC as a proxy for monitoring land-use-induced changes in soil functions related to C and N cycling.

Highlights

- Effects of conversion from potato crops to eucalyptus and fallow on soil properties and processes were assessed.
- Under eucalyptus, soil respiration increased; metabolic diversity and N transformations decreased.
- Short fallow periods did not result in soil fertility restoration.
- Hot water extractable C was the best indicator of changes in soil processes.

KEYWORDS

Bolivia, *Eucalyptus globulus*, hot water extractable carbon, microbial activity, microbial biomass, *Solanum tuberosum*

1 | INTRODUCTION

Soils are a central component of ecosystems, and the effects of land-use changes on soils have traditionally been assessed through their physicochemical and biological properties (i.e., texture, chemistry, mass and abundance of organisms). These properties are determined by the basic constituents of the soils, mineral particles, organic matter, water and air. Recently, more emphasis has been placed on soil functioning, which refers to the ability of a soil to perform multiple soil functions, such as, for example, filtering of acids and pollutants, habitat provision, water cycle regulations and nutrient cycling. Soil functions result from the interaction of soil properties and processes (Greiner, Keller, Grêt-regamey, & Papritz, 2017), and they are related to ecosystem services and human benefits, as illustrated in the "Cascading framework" (Greiner et al., 2017; Haines-Young & Potschin, 2008).

Soil physicochemical properties (e.g., microbial biomass, soil organic carbon, texture, pH and cation exchange capacity), microbial processes (e.g., carbon (C) and nitrogen (N) mineralization) and their interactions are used to assess soil functioning in relation to nutrient cycling (Brussaard, 2012; Wurst, De Deyn, & Orwin, 2012). Although total soil organic matter and carbon are widely used indicators for assessing soil responses to land-use change, they are relatively insensitive to short-term changes (Muscolo, Panuccio, Mallamaci, & Sidari, 2014; Muscolo, Settineri, & Attinà, 2015). Furthermore, soil organic matter can be composed of 70%–80% of a stable pool that is resistant to microbial decomposition and might not be relevant for nutrient cycling (Haynes, 2005). In contrast, labile carbon fractions, such as microbial biomass, and water extractable carbon and nitrogen, act as substrates for microbial activity, and may be more relevant indicators for soil functions related to nutrient cycling (Haynes, 2005), but their use remains limited.

Alterations in physicochemical soil characteristics due to land-use change will determine whether and to what extent microbial processes take place, which in turn will affect overall soil functions related to nutrient cycling. For example, agricultural land use may reduce soil organic matter, with a subsequent decrease in carbon mineralization rates (Beheshti, Raiesi, & Golchin, 2012; Paolini Gómez, 2018; Wang, Xiao, Zhang, & Wang, 2013), whereas increased nitrogen availability from fertilization may promote nitrogen transformations (Meinl, Sattolo, Mariano, Nastaro, & Otto, 2017). Conversion to fallow or afforestation, on the other hand, may lead to soil nutrient/carbon build-up and promote carbon and nitrogen mineralization rates (Cookson et al., 2007; Zhang, Wang, Li, & Han, 2008). However, the response of soil processes to land use are context specific and dependent on the relative importance of soil physicochemical properties in driving processes. The assessment of the relationships between soil properties and processes under different land uses is thus essential to achieve sustainability, as stated within the World Soil Charter (FAO & ITPS, 2015).

In the high mountainous areas of the mesothermic valleys of Bolivia (eastern branch of the Andes range), agriculture is the main professional activity for about 71% of the rural population (INE, 2015), with potato (*Solanum tuberosum* L.) as the main crop. During the last decades, these agricultural systems have been subjected to land-use change and intensification due to population increase and higher global food demand (Kessler & Stroosnijder, 2006). Changes include field subdivisions, increased cropping frequency and the dependency on external fertilizer inputs for managing soil fertility (Kessler & Stroosnijder, 2006; Pestalozzi, 2000; Pijnenborg, 1998). Furthermore, *Eucalyptus globulus* L. varieties adapted to the Andean climate were introduced to diversify farmers' incomes (Patiño, 2014), reducing the land available for annual crop cultivation, and contributing to the pressure on remaining arable soils. Concomitantly, the traditional farming method characterized by three to four cultivation cycles followed by long fallow periods of 10–20 years (de Sivila & Hervé, 1994; Pestalozzi, 2000; Zimmerer, 1993) was abandoned, and fallow periods were shortened to less than 6 years. Negative consequences of such agricultural intensification have been reported, for instance the increased risk of soil erosion, and reduced soil fertility and crop yields (Kessler & Stroosnijder, 2006). As the current fallow periods have been shortened, they may not be sufficient for soil fertility restoration. Indeed, the time needed for nutrient restoration varies across elements; nitrogen may be restored within 2 years, whereas cations may require more than 15 years (Styger & Fernandes, 2006; Szott & Palm, 1996). Moreover, although eucalyptus may contribute to soil organic carbon buildup and decreased soil erosion (Barros Soares, da Silva, Nogueira De Sousa, De Almeida, & Ribeiro da Silva, 2019; Jaleta, Mbilinyi, Mahoo, & Lemenih, 2017), it may also cause soil acidification and nutrient depletion (Leite, Silva, Ferreira, de

Barros, & Lima, 2010), or induce allelopathic effects on plants and microorganisms (Cermelli, Fabio, Fabio, & Quaglio, 2008; Zhang & Fu, 2010). So far, the information available for the agricultural highland ecosystems in Bolivia focuses on soil physicochemical parameters only, and information on the effect of land uses on soil properties and microbial processes is missing. Given the importance of these ecosystems in supporting food security for the country, an assessment of the current soil properties and processes under the main land uses is needed to provide data to help in the decision-making process of future soil management practices.

The aims of this study were to assess differences in soil functions related to carbon and nitrogen cycling following the conversion of potato crops to fallow fields and to eucalyptus plantations in agricultural highlands of the Central Andes. To assess soil function, we evaluated the associations between soil properties and microbial processes related to carbon and nitrogen mineralization. We hypothesized that soil properties and microbial processes would be similar in potato crops and fallow fields because the fallow periods are now too short to induce significant soil improvement, and that eucalyptus might lead to organic matter buildup, soil acidification and reduced nitrogen mineralization. Also, we hypothesized that labile water extractable fractions might be better indicators of soil microbial processes than total soil organic matter content.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted in the fields of the Chullchunqani Community (17°32′30″-17°33′30” S, 065°20′08″-065°21′36″ W; Figure 1), which belongs to a

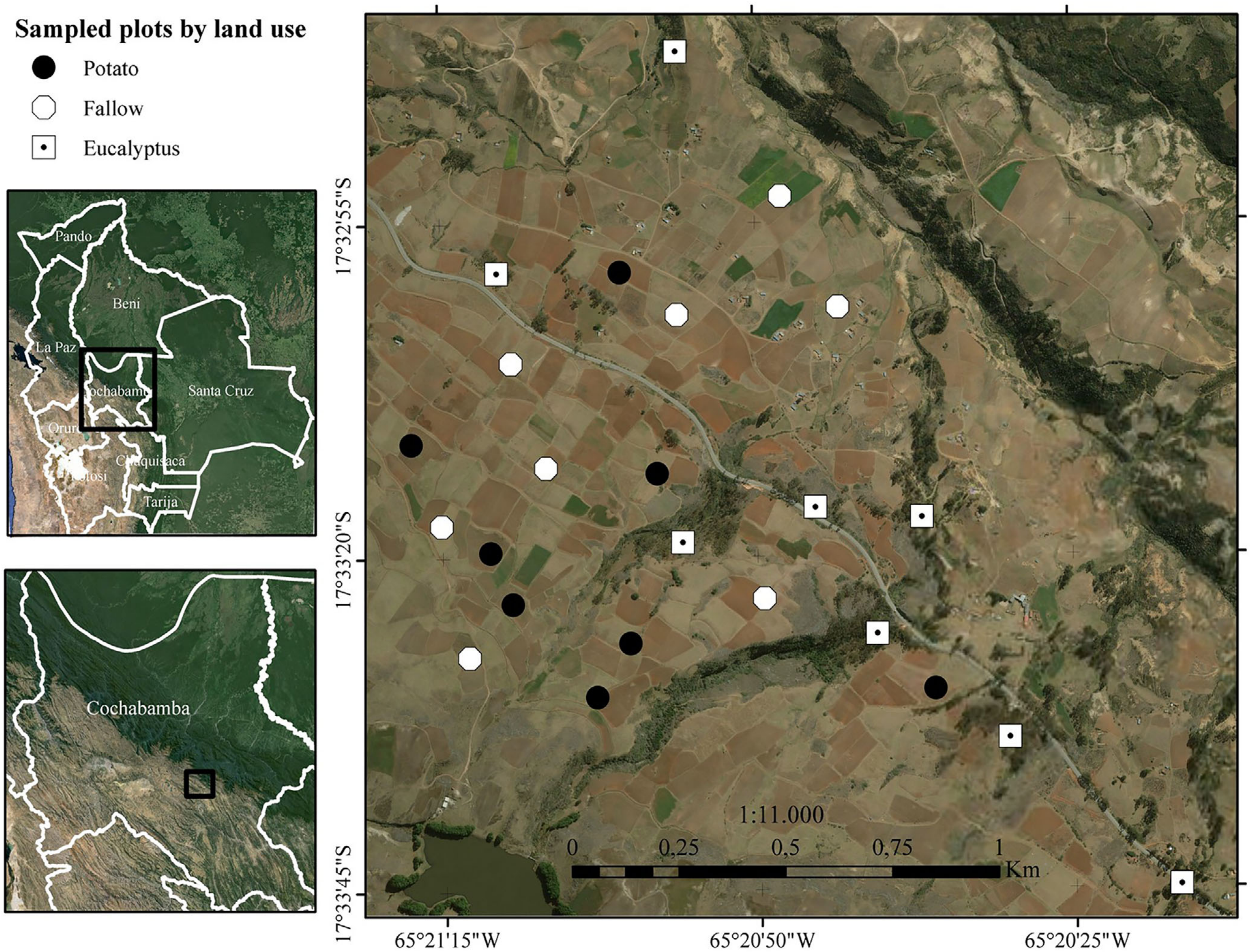

FIGURE 1 Satellite image of the study area. Location of the potato, fallow and eucalyptus plots in the Chullchunqani Community, which belongs to the agricultural region of Pocona Municipality (Cochabamba-Bolivia) [Color figure can be viewed at wileyonlinelibrary.com]

traditional agricultural region that encompasses ca. 7,000 Quechua-speaking potato farmers. The community (ca. 50 families) has an organizational structure for strategic decision-making concerning potato production as part of economic risk-minimizing strategies (Ellis-Jones & Mason, 1999). The study site is located in the Puna biogeographic province in the Eastern branch of the Andes range, at an altitude of 3,100–3,400 m a.s.l. (Navarro & Maldonado, 2002), with soils classified as Cambisols (Ministerio de Medio Ambiente y Agua, 2014). The region is characterized by a summer rainy season (November–March) and a winter dry season (April–October) (Navarro & Maldonado, 2002; Pestalozzi, 2000), with a mean annual rainfall of 500.7 mm and a mean annual temperature of 17.9°C (SENAMHI, 2016). During the winter season, average precipitation is low (16.0 mm), average temperature is 16.0°C, and frost events can take place (SENAMHI, 2016).

These climatic conditions determine the rotation cycle: potato (*Solanum tuberosum* L.) is grown mainly during the rainy season (Coûteaux, Hervé, & Mita, 2008) and secondary crops (*Vicia faba* L., faba beans; *Hordeum vulgare* L., barley) during the dry season (a rotation calendar is included in Supporting Information S1; Condori, Devaux, & Mamani, 1997). Potato fields are tilled (ca. 20 cm depth) for soil preparation, and industrial nitrogen (N), phosphorus (P) and potassium (K) fertilizer inputs as well as chicken manure (average N, P, and K content: 3.5%, 2% and 2.6%, respectively) are added at planting. Additional fertilization and irrigation are applied in varying amounts according to farmers' personal judgements, and harvesting is conducted manually. Before conversion to fallow or to eucalyptus plantations, plots were managed as cultivated fields. When converted to fallow the remaining aboveground biomass is incorporated by tillage and the fields are then left unmanaged. Fields converted to eucalyptus plantations are not managed after seedling plantation. The conversion of crops to eucalyptus plantations was not restricted to low-fertility fields.

Potato, fallow and eucalyptus fields are interspersed within the landscape in areas of ca. 0.5–1 ha, defined here as "plots". Twenty-four plots (eight plots of each land-use type) were selected within an area of ca. 4 km^2, based on the following criteria: potato plots, in which potato had been grown during the last rainy season (2016–2017); fallow plots (2–6 years old), in which the spontaneously grown vegetation (grassland of semi-arid high Andes) fully covered the soil; and forested plots with *Eucalyptus globulus* (5–25 years old). Soils were sampled at the end of the rainy season (February 2017), 2–3 weeks after harvesting in the potato plots. Each plot was divided into 10-m quadrants; three were randomly selected and designated as sampling points. At each sampling point, one composite soil sample was taken with a shovel (one central sample and four individual samples taken at two metres distance from the central sampling point; 20 cm depth), leading to a total of 72 soil samples. In order to compare similar soil layers, the thin organic layer (<0.5 cm) of the eucalyptus plots was discarded. Samples were homogenized, sieved (2 mm mesh) and stored at 4°C.

2.2 | Soil properties

General soil characteristics (soil texture; water holding capacity [WHC]) were measured on one of the three samples taken from each plot (n = 8 for each land use). Soil texture was determined with the Bouyoucos hydrometer method for particle size determination (Bouyoucos, 1927; McKean, 1993). WHC was estimated by the Shaw's method (Jenkinson & Powlson, 1976).

All other analyses were performed on all 72 samples (three samples per plot). Gravimetric moisture content was determined by weight difference of 5 g of fresh soil samples dried at 105°C for 4 h (Allen, 1989). Soil pH_{KCl} was determined with a pH meter (HI2550 HANNA instruments) in 15 g fresh soil on a 1:2 (w/v) soil to KCl 1 M solution ratio (Allen, 1989). Soil organic matter (SOM) was determined on oven-dried samples by loss-on-ignition at 450°C overnight, and total organic carbon was calculated as 58% of SOM (Allen, 1989). Water extractable carbon and nitrogen were determined using a sequential extraction, first at room temperature, followed by a second extraction at 80°C. Water soluble carbon and nitrogen were extracted from 10 g fresh soil, with 60 mL distilled water at room temperature (Ghani, Dexter, & Perrott, 2003). The soil solutions were agitated (120 rpm, 30 min), centrifuged (2704 g, 10 min), and the supernatants were filtered and stored for chemical analyses. The remaining soil was resuspended in 60 mL distilled water, and placed in an oven at 80°C for 16 h to determine the hot water extractable carbon and nitrogen (Ghani et al., 2003). Solutions were agitated and centrifuged as described above. The water soluble organic carbon (WSC) and hot water extractable organic carbon (HWC) were determined by measuring the total organic carbon in the extracts with a total carbon analyser (UV-persulfate method, Lab Toc, Pollution and Process Monitoring, UK). The NH_4^+-N, NO_3^--N and total nitrogen in the extracts were analysed colorimetrically using a continuous flow analyzer equipped with a UV digestor (AutoAnalyzer 3, BranLuebbe, Germany) for water soluble total nitrogen (WSN_{tot}) and hot water extractable total nitrogen (HWN_{tot}) determination. Water soluble organic nitrogen (WSN_{org}) was calculated as the difference between the total and mineral N (NH_4^+-N, NO_3^--N). As mineral nitrogen is mostly removed in the first extraction step, and as NH_4^+ in hot water extracts may result from the hydrolysis of organic N (Gregorich, Beare, Stoklas, & St-Georges, 2003), we assumed that all HWN_{tot} derived from organic N. Therefore, we used WSN_{org} and HWN_{tot} in our data analyses.

Exchangeable base cations (Ca^{2+}, K^+, Mg^{2+} and Na^+) and Al^{3+}, Fe^{3+} and Mn^{2+} were determined with the barium chloride extraction method (Hendershot & Duquette, 1986). Four grams fresh soil were shaken with 40 mL 0.1 M $BaCl_2$ (30 min at 180 rpm), filtered and the extracts were analysed with an inductively coupled plasma atomic emission spectrometer (VARIAN Vista). Exchangeable base cations (EBC) were computed as the sum of Ca^{2+}, K^+, Mg^{2+} and Na^+. Extractable phosphorous was estimated with the $NaHCO_3$ extraction (Brookes, Powlson, & Jenkinson, 1982; Horta & Torrent, 2007) of the non-fumigated samples for the determination of soil microbial biomass P (see below).

Soil microbial biomass carbon (MBC), nitrogen (MBN) and phosphorus (MBP) were determined with the chloroform fumigation extraction method (Brookes et al., 1982; Vance, Brookes, & Jenkinson, 1987). Fumigation of soil subsamples was carried out for 3 days in a vacuum desiccator with alcohol-free chloroform. For MBC and MBN, 10 g soil of fumigated and non-fumigated samples were extracted with 50 mL 0.5 M K_2SO_4 (1 h shaking at 180 rpm and filtration through Whatman filter #42 paper). Organic carbon in the extracts was measured with a total organic carbon analyser (Lab Toc, Pollution and Process Monitoring), and total nitrogen was analysed colorimetrically using a continuous flow analyser equipped with a UV digestor (AutoAnalyzer 3, BranLuebbe, Germany). For MBP, 8 g soil of fumigated and non-fumigated samples were extracted with 40 mL of 0.5 M $NaHCO_3$ (45 min shaking at 120 rpm and filtration through Whatman filter #42 paper). Extractable phosphorus in the solutions was analysed with an inductively coupled plasma atomic emission spectrometer (VARIAN Vista). MBC, MBN and MBP were calculated as the difference between fumigated and non-fumigated samples, with a conversion factor of 0.45 for MBC (Joergensen, 1996), 0.54 for MBN (Brookes, Landman, Pruden, & Jenkinson, 1985) and 0.4 for MBP (Brookes et al., 1982). The MBC:MBN, MBC:MBP and MBN:MBP ratios were calculated on a molar basis.

2.3 | Soil microbial processes

The soil respiration potential was measured as CO_2-C accumulation in the headspace (125 mL) of an amber bottle (Supelco, USA) from 20 g fresh soil, at 20°C in the dark after an overnight pre-incubation (Robertson et al., 1999). Gas samples (4 mL) were taken at 0, 120, 150, 180 and 210 min with an airtight syringe (Hamilton Model 1005) and analysed with an infrared absorption gas analyser (EGM-4 PPsystem, UK). The respiration potential was estimated by linear regression of CO_2-C against time. The microbial quotient (qmic, an indicator of soil C availability to microorganisms; Anderson, 2003) was calculated by dividing the microbial biomass carbon by the total organic carbon content estimated as 58% of SOM (Allen, 1989). The metabolic quotient (qCO_2, an indicator of the quantity of respired CO_2-C per unit of soil microbial biomass, reflecting maintenance energy requirement) was calculated by dividing the respiration potential by MBC (Anderson, 2003; Anderson & Domsch, 1989, 1990).

Nitrogen transformations driven by soil microorganisms were assessed with an aerobic laboratory incubation essay (Hart, Nason, Myrold, & Perry, 1994). Nitrogen was extracted from 15-g subsamples of fresh soil with 1 M KCl solution (1:5; w:v), after 1 h agitation at 180 rpm and centrifugation at 4000 rpm. In parallel, 15-g subsamples of fresh soil, adjusted to 60% water holding capacity, were incubated in the dark at 20 °C for 28 days. The water loss was monitored gravimetrically and compensated for by adding distilled water as necessary. At the end of the incubation period, nitrogen was extracted as described above. Extracts were analysed colorimetrically for NH_4^+-N and NO_3^--N using a continuous flow analyser equipped with a UV digestor (AutoAnalyser3, BranLuebbe, Germany). Net nitrogen mineralization (Nmin) and net nitrification were calculated as the net increase in mineral nitrogen (NH_4^+-N and NO_3^--N) and nitrate (NO_3^--N), respectively, over the incubation period. The relative nitrification was calculated as the percentage of NO_3^--N produced relative to the total mineral N produced.

The metabolic potential of soil bacteria (a functional diversity, indicating the potential of soil bacteria to degrade different carbon substrates; Garland & Mills, 1991; Preston-Mafham, Boddy, & Randerson, 2002) was determined with BIOLOG Ecoplates (BIOLOG™, California) containing one control well and 31 wells with different carbon substrates and tetrazolium dye (in triplicate), which indicates bacterial respiration by changing from colourless to purple. Fungi do not respond to the EcoPlate assay because they cannot reduce the tetrazolium dye included in the substrate (Preston-Mafham et al., 2002; Zak, Willig, Moorhead, & Wildman, 1994). One gram soil was extracted with 9 mL 0.1% sodium cholate (Insam & Goberna, 2004) and diluted to 10^2, 10^3 and 10^4 with 0.85% NaCl to determine the number of colony forming units (CFU) on R2A agar (Insam & Goberna, 2004). Wells were inoculated with 100 μL of the dilution containing 1,000–2000 CFU and incubated for 72 h at 20°C. Absorbance values at 590 nm from each well were read with SynergyMx (BIOTEK instruments - USA). Blank values were subtracted from the readings of each sample, and a threshold for positive tests was defined as 0.25 absorbance units to eliminate weak positives (Garland, 1996, 1997). The overall rate of substrate utilization was estimated as the average well colour development (AWCD), calculated by the mean value of single-point absorbance readings per sample (Insam & Goberna, 2004).

2.4 | Statistical analyses

Differences of soil textural components sand, silt and clay, and WHC between land uses were assessed with simple ANOVA and Tukey tests (one sample per plot, ANOVA statistics are presented in Supporting Information S2).

The differences between land uses of all other variables (three samples per plot) were evaluated with nested ANOVA using linear mixed-effects models (LMM; Mangiafico, 2015). Models were constructed including land use as fixed effect and plot as random effect, which accounted for the non-independence of the three samples taken in each plot, and for local differences between plots (i.e., time under the specific land-use type). Logarithmic (Al^{3+}, Mg^{2+}, Mn^{2+}, HWC and respiration potential) and square root data transformations (Na^{+} and Fe^{3+}) were applied to fulfill ANOVA assumptions. Marginal R^2 ($R^2_{LMM(m)}$, variance explained by fixed effects) and conditional R^2 ($R^2_{LMM(c)}$, variance explained by both fixed and random effects) were calculated according to Nakagawa & Schielzeth (2013). The proportional variance associated with the random effect component ($R^2_{LMM(r)}$) could then be computed as $R^2_{LMM(r)} = R^2_{LMM(c)} - R^2_{LMM(m)}$, and the unexplained error was estimated as $\varepsilon = 1.0 - R^2_{LMM(c)}$ (detailed statistics are presented in Supporting Information S3). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. Post-hoc comparisons were conducted with the Tukey test for mixed-effects models (Faria, Jelihovschi, & Allaman, 2018; Mangiafico, 2015).

The overall multivariate discrimination between land uses was assessed through standardized principal component analyses (PCA) on all the variables measured (except WSN_{tot}).

To determine the relative importance of the soil properties in explaining soil microbial processes, we constructed LMM using microbial processes (potential respiration, net N mineralization and net nitrification, and AWCD) as dependent variables. Soil properties (SOM, pH_{KCl} and EBC) were used as fixed effects. As the different carbon fractions were highly correlated (Supporting Information S4), separate models were constructed using pH_{KCl} and EBC, with either SOM, HWC or MBC. For net N mineralization and net nitrification, one model including HWN_{tot} instead of HWC was also fitted. The HWC:HWN_{tot} ratio was not included as an explanatory variable because the range of values was limited, all values were below the critical threshold of 20 and their individual correlations with soil processes were not significant. To account for the dependence of the three samples taken within each plot, and the dependence of samples within each land use, both levels were included as random effects. Models were fitted using REML estimation, and the marginal r-square $R^2_{LMM\,(m)}$ (variance explained by fixed effects) and semi-partial R^2_i (variance explained by an individual predictor while adjusting for the other predictors in the model) were calculated according to Jaeger, Edwards, Das, and Sen (2016).

Statistical analyses were conducted with the R software 3.6.1 (R Core Team, 2018) using the packages "car" (Fox & Weisger, 2011), "nlme" (Pinheiro et al., 2018), "mgcv" (Wood, 2017), "TukeyC" (Faria et al., 2018), "multcomp" (Hothorn et al., 2017), "multcompView" (Graves, Piepho, & Selzer, 2015), "MuMIn" (Barton, 2018), "r2glmm" (Jaeger et al., 2016) and "factoextra" (Kassambara & Mundt, 2019).

3 | RESULTS

3.1 | Soil properties

For the general characterization of soils (Table 1), WHC and texture, no significant differences were found between land uses.

The SOM content, measured by loss-on-ignition, was significantly higher under eucalyptus plantations compared to potato and fallow plots, and ranged from 55.5 to 144.4 g kg^{-1} (Table 2). The soil exchangeable cations were dominated by Ca^{2+} (61%), Mg^{2+} (26%) and K^{+} (11%), with significantly lower values of Ca^{2+} and K^{+} under eucalyptus compared to potato plots. Na^{+} accounted for less than 1% of exchangeable cations and did not show differences between land uses. Exchangeable Al^{3+} was significantly higher under eucalyptus, accounting for 17% of exchangeable cations compared to potato and fallow plots, where Al^{3+} accounted for 3% to 4%. The remaining cations Fe^{2+} and Mn^{2+} had significantly higher values under eucalyptus. The $NaHCO_3$ extractable P and the sum of exchangeable base cations (EBC) were significantly lower under eucalyptus plantations compared to potato and fallow plots. Soil pH_{KCl} and exchangeable Mg^{2+} were not significantly different between land uses (Table 2).

HWC was significantly higher under eucalyptus plantations compared to potato and fallow plots (Table 2). On average, the contribution of HWC to the total water

TABLE 1 Mean values ± standard deviation of sand, silt and clay fractions and water holding capacity (WHC).

	Potato	Fallow	Eucalyptus
Sand (%)	21.8 ± 4.8 a	22.9 ± 4.3 a	34.1 ± 9.6 a
Silt (%)	29.5 ± 3.9 a	31.6 ± 8.8 a	29.5 ± 5.0 a
Clay (%)	48.7 ± 5.9 a	45.6 ± 11.3 a	36.4 ± 6.3 a
WHC (%)	51.2 ± 4.0 a	53.2 ± 2.6 a	48.8 ± 7.7 a

Note: Different letters indicate significant differences between land uses ($p < 0.05$, $n = 8$, ANOVA and Tukey).

extractable C (HWC + WSC) was 95, 93 and 93% under eucalyptus, fallow and potato plots, respectively. HWC represented 2.13, 1.66, and 1.54% of total organic carbon (calculated as 58% of SOM; Allen, 1989) under eucalyptus, fallow and potato plots, respectively. The HWN_{tot} fraction in eucalyptus and fallow plots accounted for 84 and 72% of total extractable N (WSN_{tot} + HWN_{tot}), with significantly lower values in potato plots, where it accounted for 54% of total extractable N. On average, the WSN_{tot} was composed of 13, 3 and 2% of NH_4^+-N, and 55, 79 and 90% of NO_3^--N under eucalyptus, fallow and potato plots,

TABLE 2 Mean values ± standard deviation of soil properties.

Soil chemistry	Potato	Fallow	Eucalyptus
pH_{KCl}	4.34 ± 0.28 a	4.30 ± 0.30 a	3.96 ± 0.23 a
SOM (g kg^{-1})	86.98 ± 13.85 b	78.22 ± 12.90 b	106.87 ± 25.27 a
EBC ($cmol_c$ kg^{-1})	8.22 ± 1.00 a	7.17 ± 2.00 a	5.85 ± 2.60 b
Ca^{2+} ($cmol_c$ kg^{-1})	5.23 ± 0.28 a	4.69 ± 0.53 ab	3.55 ± 0.75 b
K^+ ($cmol_c$ kg^{-1})	0.88 ± 0.13 a	0.87 ± 0.12 a	0.52 ± 0.08 b
Mg^{2+} ($cmol_c$ kg^{-1})	2.05 ± 0.07 a	1.60 ± 0.16 a	1.70 ± 0.19 a
Na^+ ($cmol_c$ kg^{-1})	0.07 ± 0.01 a	0.02 ± 0.01 b	0.08 ± 0.01 a
Fe^{3+} ($cmol_c$ kg^{-1})	$1.29 \times 10^{-03} \pm 7.71 \times 10^{-04}$ a	$1.83 \times 10^{-03} \pm 8.95 \times 10^{-04}$ ab	$2.88 \times 10^{-03} \pm 1.66 \times 10^{-03}$ b
Mn^{2+} ($cmol_c$ kg^{-1})	$1.04 \times 10^{-02} \pm 5.32 \times 10^{-03}$ a	$1.08 \times 10^{-02} \pm 7.17 \times 10^{-03}$ a	$2.42 \times 10^{-02} \pm 1.47 \times 10^{-02}$ b
Al^{3+} ($cmol_c$ kg^{-1})	0.23 ± 0.05 b	0.28 ± 0.03 b	1.19 ± 0.37 a
Extractable P (mg kg^{-1})	63.47 ± 18.66 a	38.69 ± 8.42 b	18.59 ± 8.02 c
Water extractable carbon and nitrogen			
HWC (mg C kg^{-1})	774.00 ± 129.49 b	750.80 ± 186.16 b	1,367.00 ± 557.44 a
HWN_{tot} (mg N kg^{-1})	67.63 ± 13.00 a	65.44 ± 13.14 a	84.20 ± 21.30 a
HWC:HWN_{tot} ratio	11.58 ± 1.00 b	11.38 ± 1.03 b	15.68 ± 2.42 a
WSC (mg C kg^{-1})	56.67 ± 16.58 a	55.23 ± 17.76 a	69.41 ± 19.59 a
WSN_{tot} (mg N kg^{-1})	55.81 ± 16.74 a	25.36 ± 7.50 b	19.116 ± 12.05 b
WSN_{org} (mg N kg^{-1})	3.50 ± 1.89 a	4.39 ± 0.84 a	4.15 ± 1.95 a
WSC:WSN_{org} ratio	15.29 ± 5.13 ab	12.50 ± 2.83 b	18.88 ± 6.64 a
Soil microbial biomass			
MBC (mg C kg^{-1})	350.22 ± 42.20 b	333.10 ± 67.76 b	599.97 ± 200.31 a
MBN (mg N kg^{-1})	53.56 ± 13.17 b	63.37 ± 14.06 b	118.20 ± 34.57 a
MBP (mg P kg^{-1})	5.25 ± 1.83 c	12.38 ± 8.75 b	18.71 ± 2.31 a
MBC:MBN	8.67 ± 2.90 a	6.53 ± 2.34 ab	5.85 ± 0.56 b
MBC:MBP	238.16 ± 245.82 a	135.29 ± 106.55 a	104.53 ± 74.71 a
MBN:MBP	30.54 ± 28.26 a	19.37 ± 13.17 a	17.56 ± 11.58 a
MBC:MBN:MBP	238:31:1	135:19:1	105:18:1

Note: Values were calculated using average values of the three samples per plot ($n = 8$). Different letters indicate significant differences between land uses ($p < 0.05$, nested ANOVA using linear mixed-effects models and Tukey tests).

Abbreviations: EBC, exchangeable base cations; extractable P, $NaHCO_3$ extractable phosphorus; HWC, hot water extractable carbon; HWN_{tot}, hot water extractable nitrogen; MBC, soil microbial biomass carbon; MBN, soil microbial biomass nitrogen; MBP, soil microbial biomass phosphorus; SOM, soil organic matter; WSC, water soluble carbon; WSN_{org}, water soluble organic nitrogen; WSN_{tot}, water soluble total nitrogen.

respectively. WSN_{org} accounted for 6.7, 17.3 and 21.7% of WSN_{tot} in potato, fallow and eucalyptus plots. HWC:HWN_{tot} and WSC:WSN_{org} were significantly higher under eucalyptus plantations compared to potato and fallow soils. We did not find a significant difference between land uses for WSC, WSN_{tot}, WSN_{org} and HWN_{tot} (Table 2).

MBC ranged from 156.0 to 948.0 mg C kg^{-1}, and MBN ranged from 28.3 to 180.7 mg N kg^{-1}; both were significantly higher in eucalyptus plots. MBP values were below the detection limit for some soil samples in potato plots, and significantly higher values were recorded in eucalyptus plantations, with a maximum of 31.7 mg P kg^{-1}. The MBC:MBN molar ratio ranged from 3.0 to 13.5, with significantly lower values under eucalyptus compared to potato soils. The MBC:MBP and MBN:MBP had considerably higher variation and did not show significant differences between land uses.

3.2 | Soil microbial processes

Soil respiration potential ranged between 0.15 and 1.07 µg CO_2-C h^{-1} g^{-1}, with the highest mean values under eucalyptus plots compared to fallow and potato plots (Figure 2). The microbial quotient, qmic, ranged from 3.84 up to 12.37 mg MBC g^{-1} soil C, with higher values in eucalyptus plantations compared to potato and fallow plots, whereas the metabolic quotient, qCO_2, ranged from 0.51 to 1.57 µg CO_2-C h^{-1} mg^{-1} C, with significantly higher values in eucalyptus and fallow plots. Net N mineralization and net nitrification were significantly lower under eucalyptus and fallow compared to potato plots. Net NO_3^--N production accounted for 96% of the total net mineral nitrogen produced in potato and fallow soils, whereas it accounted for 59% under eucalyptus. The metabolic potential of soil bacteria (AWCD) had significantly lower values in eucalyptus plantations compared to potato and fallow soils.

3.3 | Relationships of soil properties and soil processes

The PCA showed multivariate discrimination of eucalyptus from potato land use, whereas fallow land use was intermediate (Figure 3). The variable loadings indicated that eucalyptus land use was associated with labile C and N fractions, respiration potential and exchangeable Al, Fe and Mn. Potato land use was associated with high net N transformation rates, WSN_{tot}, exchangeable base cations, extractable P and pH_{KCl}.

The results of statistical modelling to examine the relative importance of soil properties in explaining soil

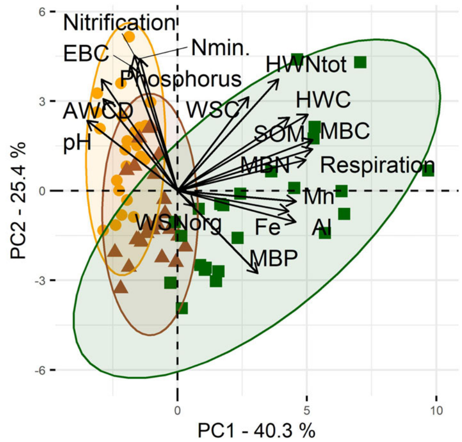

FIGURE 2 Multivariate analyses (principal component analyses) conducted on the soil properties and processes of the soil samples from the potato (●), fallow (▲) and eucalyptus (■) land uses. For each land use the 95% confidence ellipses are shown. AWCD, average well colour development; EBC, exchangeable base cations; HWN_{tot}, hot water extractable total nitrogen; HWC, hot water extractable carbon; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; MBP, microbial biomass phosphorus; SOM, soil organic matter; WSC, water soluble carbon; WSN_{org}, water soluble organic nitrogen; Nmin, net nitrogen mineralization; Respiration, respiration potental; Phosphorous, extractable phosphorous; Fe, Mn, and Al, extrcatable iron, manganese and aluminium; pH, pH_{KCl} [Color figure can be viewed at wileyonlinelibrary.com]

processes are presented in Table 3. pH_{KCl} and EBC were only statistically significant for AWCD. None of the carbon fractions (SOM, HWC and MBC) was a significant predictor of AWCD. Model fit was around $R^2_{LMM(m)} = 0.4$ for all AWCD models, with a relatively higher contribution of pH_{KCl} compared to EBC for two of the models. Respiration potential, net nitrogen mineralization and net nitrification showed best model fit with HWC. HWC was the best predictor for respiration potential ($R^2_{LMM(m)} = 0.81$), followed by MBC ($R^2_{LMM(m)} = 0.66$) and SOM ($R^2_{LMM(m)} = 0.37$). For net N mineralization and net nitrification, HWC and HWN_{tot} were the best predictors (HWC: $R^2_{LMM(m)} = 0.49$ and 0.50; HWN_{tot}: $R^2_{LMM(m)} = 0.47$ and 0.54, respectively), followed by SOM ($R^2_{LMM(m)} = 0.31$ and 0.33) and MBC ($R^2_{LMM(m)} = 0.17$ and 0.19).

4 | DISCUSSION

4.1 | Effects of eucalyptus plantations on soil properties and processes

Plantation of eucalyptus on fields previously cultivated with potato led to an increase in SOM, labile carbon fractions (HWC and MBC), HWC:HWN_{tot}, exchangeable Al

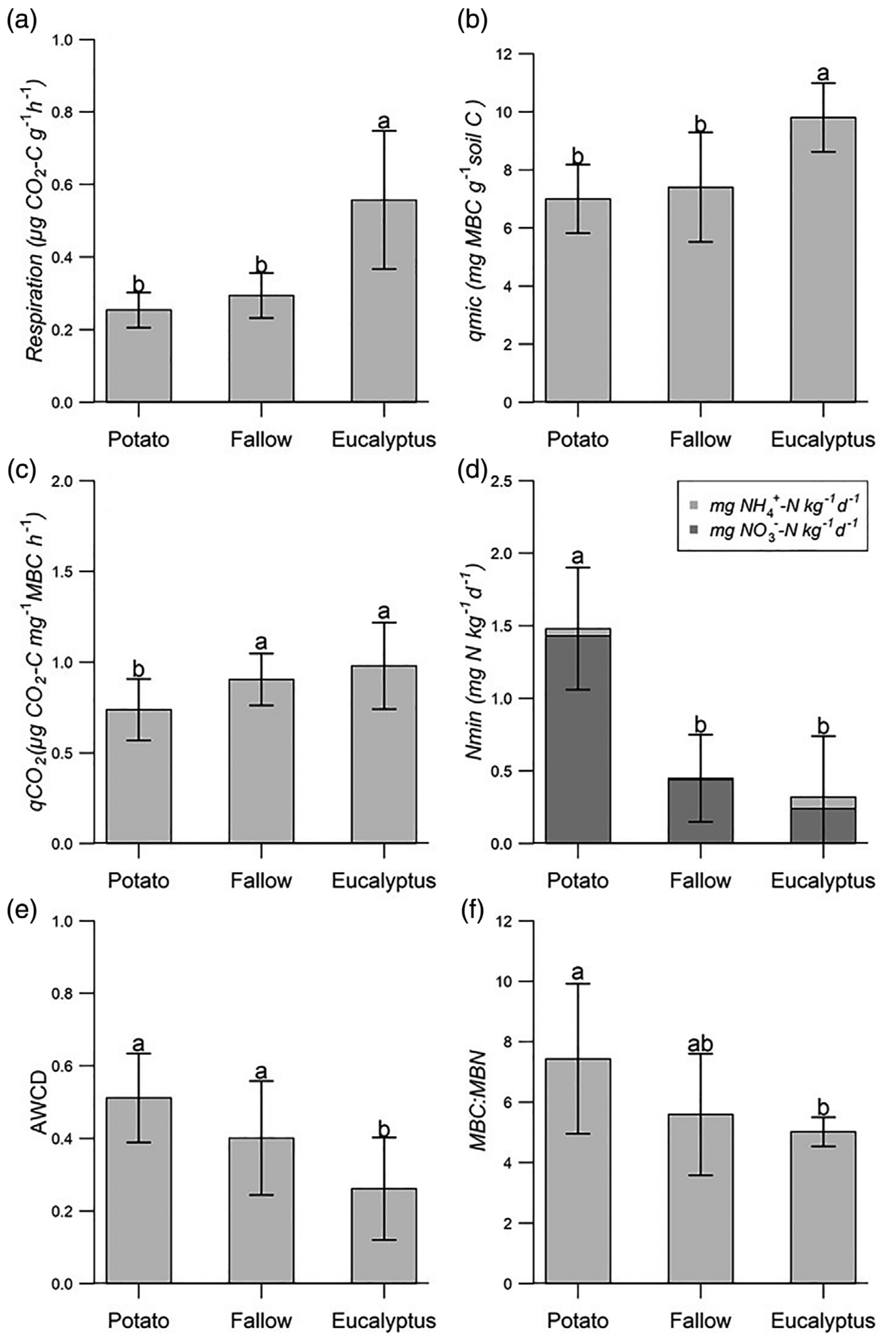

FIGURE 3 Soil processes and related parameters under potato, fallow and eucalyptus land uses. (a) Respiration potential, (b) microbial quotient (qmic), (c) metabolic quotient (qCO_2), (d) net N mineralization and net nitrification, (e) average well colour development (AWCD), and (f) microbial carbon-to-nitrogen ratio. Mean values and standard deviations were calculated using average values of the three samples per plot ($n = 8$). Different letters indicate significant statistical differences ($p < 0.05$, nested ANOVA using linear mixed-effects models and Tukey tests)

and respiration potential, and a decrease in EBC, Nmin, net nitrification and AWCD. Previous studies also showed an increase in SOM and water extractable C fractions under eucalyptus plantations compared to pasture soils and cultivated areas (Bai & Blumfield, 2015; Kumar, Mishra, Chaudhari, & Basak, 2018). This can be explained by (a) the higher amount of litter returning to the soil under eucalyptus (Chantigny, 2003; van Leeuwen, Djukic, Bloem, Lehtinen, & Hemerik, 2017), and (b) lower organic matter oxidation compared to potato and fallow plots, where previous tillage and potato harvesting may have caused aggregate breakdown and increased decomposition (Islam & Weil, 2000). The higher SOM and labile carbon fractions were related to an increase in soil respiration potential, as illustrated by their positive relationships. Our results indicated a higher substrate availability (higher qmic) compared to potato plots, but increased microbial energy maintenance demands (higher qCO_2) indicate lower substrate quality (Anderson & Domsch, 1990; Thirukkumaran & Parkinson, 1999). The reduced metabolic potential of soil bacteria (AWCD) under eucalyptus also indicates lower quality substrate (greater content of compounds with low biodegradability, e.g., lignin), despite the increase of

TABLE 3 Results of linear mixed-effects modelling to determine the strength of association between soil properties and soil processes.

	Respiration potential		Net nitrogen mineralization		Net nitrification		AWCD	
Set 1: SOM								
$R^2_{LMM(m)}$	0.37		0.31		0.33		0.44	
	R^2_i	Est.	R^2_i	Est.	R^2_i	Est.	R^2_i	Est.
SOM	0.29	0.003**	0.17	0.01*	0.18	0.01**	0.01	-4.80×10^{-04}
pH_{KCl}	0.01	0.04	0.00	0.05	0.00	−0.05	0.09	0.17*
EBC	0.00	−0.001	0.02	0.04	0.03	0.04	0.09	0.02*
Set 2: HWC								
$R^2_{LMM(m)}$	0.81		0.49		0.50		0.41	
	R^2_i	Est.	R^2_i	Est.	R^2_i	Est.	R^2_i	Est.
HWC	0.78	2.6×10^{-04}**	0.40	7.4×10^{-04}*	0.41	7.1×10^{-04}*	0.01	2.7×10^{-05}
pH_{KCl}	0.00	8.2×10^{-04}	0.01	−0.19	0.01	−0.17	0.14	0.19*
EBC	0.00	6.8×10^{-04}	0.03	0.04	0.04	0.04	0.08	0.01*
Set 3: MBC								
$R^2_{LMM(m)}$	0.66		0.17		0.19		0.40	
	R^2_i	Est.	R^2_i	Est.	R^2_i	Est.	R^2_i	Est.
MBC	0.61	5.9×10^{-04}**	0.06	7.2×10^{-04}	0.07	7.4×10^{-04}	0.01	8.3×10^{-05}
pH_{KCl}	0.00	6.5×10^{-03}	0.01	−0.22	0.01	−0.20	0.14	0.20**
EBC	0.00	3.2×10^{-03}	0.07	0.07*	0.08	0.07	0.08	0.02*
Set 4: HWN_{tot}								
$R^2_{LMM(m)}$	-		0.47		0.54		-	
	-	-	R^2_i	Est.	R^2_i	Est.	-	-
HWNtot	-	-	0.39	0.02**	0.46	0.02**	-	-
pH_{KCl}	-	-	0.04	−0.29	0.04	−0.27	-	-
EBC	-	-	0.01	0.03	0.02	0.02	-	-

Note: Models fitted with soil pH_{KCl}, exchangeable base cations (EBC) and either soil organic matter (SOM), hot water carbon (HWC) or microbial biomass carbon (MBC) as explanatory variables (set 1–3). For net N mineralization and net nitrification hot water extractable nitrogen (HWN_{tot}) was also included as explanatory variable (set 4). Four different sets of models were thus fitted, and for each set the parameter estimates (Est.) are presented, and the marginal $R^2LMM_{(m)}$ and semi-partial R^2_i were calculated according to Jaeger et al. (2016). AWCD, average well colour development.

$^*p < 0.05$.

$^{**}p < 0.01$.

labile carbon fractions (SOM, HWC and MBC) under these trees. A shift of the microbial community towards fungal dominance might also have occurred under eucalyptus, as indicated by the decrease in the microbial C:N ratio. However, the magnitude of change was low (mean values: 8.7 under potato, 5.8 under eucalyptus) and within the range where fungal and bacterial C:N ratios overlap (Strickland & Rousk, 2010).

Despite the absence of differences in bulk soil pH_{KCl} between land uses, the fourfold increase in exchangeable Al^{3+} and the higher exchangeable Fe^{2+} and Mn^{2+} under eucalyptus are indicative of soil acidification, possibly due to organic acids secreted by eucalyptus roots (Prosser, Hailes, Melville, Avery, & Slade, 1993). Aluminium may reduce crop growth through its phytotoxicity to roots (Al^{3+} and $Al(OH)^{2+}$; Kinraide, 1991), and through a decrease in P availability (Kretzschmar, Hafner, Bationo, & Marschner, 1991; Robarge & Corey, 1979). The absence of external P inputs may explain the three times lower $NaHCO_3$-extractable P under eucalyptus compared to soils under potato fields. Increased aluminium may also affect soil functions related to N cycling, as N mineralization and nitrification are inhibited by Al through the suppression of enzymatic activities (Kunito et al., 2016; Tietema, Warmerdam, Lenting, & Riemer, 1992). Lower C quality and Al toxicity, as well as antimicrobial and allelopathic properties of volatile oils and toxins excreted by eucalyptus (Cai et al., 2010; Cermelli et al., 2008; Chen et al., 2013) may cause microbial stress (increased energy maintenance demands, qCO2) and contribute to the lower metabolic potential of soil bacteria (AWCD) under this tree compared to potato soils. Altogether, our results indicate profound effects of eucalyptus plantations on soil properties, microbial processes and functions related to C and N cycling, which may be associated with the inability to cultivate potato after eucalyptus, as reported by local farmers (Morales & Patiño, 2008).

4.2 | Effects of fallowing on soil properties and processes

Fallow and potato land uses were similar for most soil properties, except for the higher WSN_{tot} and extractable P in fallow soils. Higher WSN_{tot} and extractable P in potato cultivated fields can be attributed to mineral and organic fertilization, and subsequent mineralization of organic fertilizers. Our data indicate that the effects of fertilization on extractable P and N decrease over short time periods (2–6 years) after the conversion to fallow soil, confirming the findings of Condori et al. (1997), who showed that the effects of chemical P additions on extractable P lasted for up to 2 years after fertilization.

Labile fractions such as MBC and MBN have been reported to increase quickly as a result of land-use change from agriculture to grassland (Carter & Rennie, 1982; Landgraf, 2001). Such changes have commonly been associated with fertility restoration, as soils that maintain a high level of microbial biomass are capable of not only storing more nutrients, but also of cycling more nutrients that are easily available to plants (Anderson & Domsch, 1980; Ghani et al., 2003; Joergensen, 2010; Stenberg, 1999). However, we did not find differences in MBC or MBN between potato and fallow soils, indicating that fallow periods of 2–6 years might not restore soil fertility. In contrast, MBP was higher under fallow soils, despite higher extractable and total P in potato soils. This is consistent with previous research, indicating that $NaHCO_3$-extractable P might not be a good indicator of P availability to plants and microorganisms, as they display adaptive mechanisms enhancing P acquisition from the soil (Brookes, Powlson, & Jenkinson, 1984; Bucher, 2006; Lambers, Raven, Shaver, & Smith, 2007). Low MBP in potato fields might be due to the higher plant competitiveness and P requirements during tuber formation/growth, resulting in low P availability to soil microorganisms (Alvarez-Sánchez et al., 1999; Castro, 2005). Conversion to fallow would then lead to increased MBP as a result of higher P availability and storage of excess P in microbial cells (Achbergerová & Nahálka, 2011; Heuck, Weig, & Spohn, 2015). These differences in MBP resulted in changes in the microbial C:N:P molar ratios, with potato soils showing the highest ratios (238:31:1), above the world average for grassland and agricultural soils (60:7:1, Cleveland & Liptzin, 2007; Hartman & Richardson, 2013), indicating potential P limitation to microbial metabolism (Hartman & Richardson, 2013).

We did not find differences in HWN_{tot} or WSN_{org} between land uses, despite the fertilization of potato crops with chicken manure and mineral N. This indicates that these external N inputs do not contribute to total or organic N accumulation (Condori et al., 1997; Hepperly, Lotter, Ulsh, Seidel, & Reider, 2009). The higher net N mineralization and nitrification rates in potato plots are likely to be due to increased substrate availability from organic fertilization and soil disturbance caused by tillage and harvesting (Li, Peng, Rae, & Zhou, 2001). Higher N turnover would increase mineral N availability for plants and microorganisms (Curtin, Wright, Beare, & Mccallum, 2006), but coupled with excessive N fertilization (FAO, 1999), it may also lead to NO_3^- leaching and groundwater contamination. This is also supported by the WSN_{tot}, which is mainly composed of NO_3^-. Upon conversion to fallow, net N mineralization and net nitrification rates would depend on the residual fertilizer and on litter returning to the soil from colonizing vegetation.

Studies of long fallow periods (>10 years) have associated fertility restoration with increased total soil C, potentially mineralizable C and N, microbial biomass and cation exchange capacity (de Sivila & Angulo, 2006; Sarmiento & Bottner, 2002). Our results indicate that the short fallow periods currently practised do not contribute to such changes. As the reduced available land and high food demands do not allow for long fallow periods, alternative sustainable practices are needed to allow high-yield potato cultivation.

4.3 | Soil carbon fractions as indicators of changes in soil microbial processes

All three carbon fractions assessed in this study (SOM, HWC and MBC) were related to the respiration potential, but HWC was the best predictor, explaining up to 81% of the variation in respiration across land uses. Similarly, Wang, Dalal, Moody, & Smith (2003) also found that extractable C fractions were better predictors than soil organic carbon for respiration of rewetted soils. The labile HWC contains more easily available substrates for microorganisms (Landgraf, Leinweber, & Makeschin, 2006) and might thus be a better indicator of soil functions related to C and N cycling than SOM and MBC.

HWC was also the best predictor for net N mineralization and net nitrification, with models explaining 49 and 50% of their variation. The lower strength of association in comparison to the respiration potential may be due to the fact that net N mineralization is the result of several gross processes and that nitrification is controlled by autotrophic microorganisms, not directly depending on soil carbon. Also, Colman and Schimel (2013) suggested that the chemical forms of organic nitrogen and their interaction with soil minerals, controlling accessibility of organic nitrogen to microorganisms, as well as potential differences in microbial community composition may be additional controls of net N mineralization. As HWC was correlated with HWN_{tot}, models including HWN_{tot} showed similar explanatory power. As reported previously (Colman & Schimel, 2013; Templer, Findlay, & Lovett, 2003), MBC was not a good predictor of net nitrogen mineralization and nitrification. The low explanatory power of MBC for net nitrification is due to the fact that the nitrifying autotrophic archaea and bacteria are less abundant than heterotrophs and represent only a fraction of total microbial biomass. Previous studies, however, reported a significant correlation between MBC and net N mineralization in forest soils (Malchair & Carnol, 2009), indicating that factors driving net N transformations may vary across ecosystems.

In contrast to respiration and N mineralization, metabolic diversity of soil bacteria was mainly related to soil pH_{KCl}, and to a lower extent to EBC, but not to labile C and N fractions. This differs from findings of Juan et al. (2015), who concluded that SOC availability under organic amendments increased metabolic diversity of soil bacteria. However, the increase of metabolic diversity with soil pH, as also documented by D'Acunto, Andrade, Poggio, and Semmartin (2018), is in agreement with the general microbial theory of positive effects of soil pH on microbial diversity (Wakelin et al., 2008; Willey, Sherwood, & Woolverton, 2017).

5 | CONCLUSIONS

Soil use and soil fertility have become a crucial issue in the Andean region due to the growing population and land-use intensification. We investigated differences in soil properties and microbial processes related to C and N cycling following the conversion of potato crops to fallow fields and to eucalyptus plantations in agricultural highlands of the Central Andes. The planting of eucalyptus on soils previously cultivated with potato caused drastic changes: respiration potential increased, whereas net N transformations, P availability and metabolic diversity of soil bacteria decreased. The traditional long fallow practice has been replaced by 2–6-year fallowing periods, which did not result in soil fertility restoration, as it did not lead to major changes in soil properties and microbial processes compared to potato crops. The labile soil carbon fractions were better indicators of soil C and N mineralization processes than SOM. Overall, our results show that the use of eucalyptus for afforestation should be considered carefully, especially in communities where agriculture constitutes the main economic income. Also, alternative management practices are needed for potato production to replace the long fallowing periods. HWC was the best indicator for soil processes and should be considered for monitoring changes in soil functions related to C and N cycling in response to land-use change.

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AUTHOR CONTRIBUTIONS

Alejandro Coca: Conceptualization; formal analysis; investigation; writing-original draft; writing-review & editing. **Jean-Thomas Cornelis:** Conceptualization; funding acquisition; supervision; writing-review & editing. **Monique Carnol:** Conceptualization; formal analysis; funding acquisition; resources; supervision; writing-original draft; writing-review & editing.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Author elects to not share data.

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